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PLUMAGE-CYCLES AND THE RELATION BETWEEN
PLUMAGES AND MOULTS.

BY JONATHAN DWIGHT JR., M.D.

THE plumage-cycle of a species is the series of successive plumages that are peculiar to the species, or it may be said that the several plumages of the young bird together with those of the adult, make up a plumage-cycle. If plumages are viewed in the natural sequence in which they succeed one another, it will be found that plumage-cycles of species vary in many details difficult to put into words, for with broadening knowledge of the subject we find that many familiar terms are inadequate. They have lost definiteness of meaning through careless use, or they have outgrown their early significance or they have been paraphrased into a host of synonyms, in any or all of these ways occasioning much confusion of ideas. Ornithology seems to be lagging behind other branches of zoölogy in the slow movement towards exactness of statement and of language, and many of the vague ideas that prevail regarding the relation of plumage to moult need to be reduced to exact terms. Some steps have already been taken in this direction, and perhaps many more need to be taken before we shall reach a firm foundation on which to build an adequate system of plumages and moults, but it seems to me the time has arrived when the prominent facts admit of a more accurate grouping than has hitherto been attempted.

Most of us are so committed to the old idea of seasonal plumages and seasonal periods of moult, that it is in the nature of a shock to realize that the seasonal idea fits neither birds of the tropics nor those of temperate regions. We are accustomed to think of the 'summer' and 'winter' dress of birds as if they all changed their feathers twice in the year. While these adjectives of season may apply to birds that actually do moult twice in the year, we are at present without a suitable word to express the plumage of birds that, wearing the same dress throughout the year, moult only once. Nor is it safe, if we wish to be accurate, to speak as we do of 'spring' and 'fall' moults, because the moulting periods vary so with species and with age that no

seasonal line may be drawn, even in countries that have springs and falls. Then again it has been customary to class as 'immature' several different stages of plumage now too well understood to permit of such lax classification. The fact is, plumages and moults have outgrown their nomenclature, as the various terms of writers clearly indicate, and while I have been in good company in sticking to the seasonal idea, I have long felt that we must come to a wider view.

We may not all agree as to what constitutes a plumage and what a moult, but we know that plumage is made up of successive generations or crops of feathers that, with the exception of the first, grow at periods of moult, and that the feathers remain, even though sadly altered by wear, until the next moult. A complete moult can only result in a simple plumage, all the feathers of the generation being of about the same age, but if the moult be partial the resulting plumage will be compound and made up of new feathers more or less mixed, according to circumstances, with those of an earlier generation. Now, it seems to me, there are three great and distinct epochs of plumage in the life-cycle of the bird corresponding in a measure to infancy, youth and manhood in the human being, and three adjectives are applicable to them, viz. natal (Lat. *natalis*), juvenal (Lat. *juvenalis*), and nuptial (Lat. *nuptialis*). The natal plumage consists of the down-like feathers of the first generation known as neossophtes, the juvenal plumage consists of feathers of the second generation, and the nuptial includes the later generations. But as a matter of fact such simplicity of plumages is rarely found; the natal plumage may be lacking, the juvenal is worn wholly or in part as a first nuptial, and the nuptial is supplemented by non-nuptial and protective stages.

From time immemorial, the adult plumage of the breeding season has been accepted as the one most typical of the species, and the moult by which it is entirely swept away forms a fixed point in every plumage-cycle. The plumage may well be called the nuptial and the moult the postnuptial. Some species at the postnuptial moult acquire an annual plumage lasting through the whole year until the next postnuptial period; other species acquire a distinctly non-nuptial plumage which, at the prenuptial moult prior

to the breeding season, becomes a true nuptial plumage, simple or compound according as the moult is complete or incomplete. It is therefore obvious that there are three plumages belonging especially to adult birds, instead of the two usually recognized if adherence be given to the seasonal idea. The three are the annual (possibly *annuo-nuptial* would express it better), the nuptial and the non-nuptial. As for the special protective plumages of the Ducks and Ptarmigans, they might be called tutelar (Lat. *tut-claris*), and they seem to be the result of a complete postnuptial moult, on the heels of which follows so quickly the always incomplete posttutelar, that the latter seems to be a continuation of the former. The Ducks, however, pass most of the year in the compound annual plumage, resulting from the two moults, while the Ptarmigans on the other hand acquire a compound non-nuptial dress that is further compounded for the breeding season by a prenuptial moult lacking in the Ducks. These then are the plumages and moults peculiar to birds in their second or later years, that is after the first postnuptial moult, and it will now be easier to understand those of the young bird that at each successive moult approaches more nearly to the ultimate adult plumage.

The first plumage of the young bird is the natal, a name applicable to the rudimentary feathers of the first generation known as neossoptiles or neoptiles. The Megapodiidæ are said to lose this plumage before the bird leaves the egg, while its growth both before and after hatching may be observed in many familiar species. Most water birds, like the Pygopodes, the Anatidæ or the Limicolæ, and among land birds the Gallinæ, are thickly covered with this down-like plumage, while its scantiness is marked in most land birds like the Passeres or Columbæ. In some families like the Picidæ or Trochilidæ it is absent. At most, the natal plumage is worn for only a brief period and is completely lost by what may be considered as a postnatal moult, although this consists chiefly of loss by abrasion of the neossoptiles from the tips of the succeeding feathers to which they are attached. There is no cessation of feather growth as after an ordinary moult, but the calamus of the neossoptile is continued into the tip of the definitive feather or teleoptile which follows. There is, however, feather loss of the first generation and feather gain of the second, the two essential constituents of a moult.

The second plumage of a young bird may be appropriately called the juvenal rather than 'juvenile,' which word has a less exact meaning; like other terms that have been in use for this plumage. The current expression 'first plumage' is entirely inappropriate for a distinctly second stage or second generation of feathers. These have been called 'mesoptiles' to distinguish them from other teleoptiles but the distinction is often not very obvious, although some of them in some species and all of them in others are weaker and softer in structure than adult feathers, and also lack, as a rule, the adult patterns and colors. The order of their growth, the types of feathers, and the areas covered, need not concern us in the present connection, although it is important to note that the remiges of the juvenal dress of land birds like the Passeres or Gallinæ, grow in advance of the body plumage, while water-birds like the Pygopodes or Anatidæ acquire most of the body plumage first. Among many of the smaller species of birds the juvenal plumage is discarded within a few weeks. There are many other species, however, both large and small that retain at least a portion of it, usually the wings and tail, for an entire year.

The postjuvenal moult is an extremely important point in every plumage-cycle and varies both in its completeness and in the time of its occurrence, even among closely related species. It has often been confused with the prenuptial moult which in some species and in some individuals it overlaps in point of time. In fact, we often find this moult so long drawn out, that in some species having also a prenuptial moult, both moults may be found in progress on the same specimen, as may be seen among some of the Longipennes, Anatidæ and Passeres. But irrespective of time of occurrence and extent of feather areas involved, two plumages result from a postjuvenal moult, the first annual (juveno-annual) or the first non-nuptial (juveno-non-nuptial) either of which may be simple or compound as the moult is complete or incomplete. The simple first annual plumage is illustrated by the English Sparrow (*Passer domesticus*), the compound by the American Robin (*Merula migratoria*), the simple non-nuptial plumage by the Horned Lark (*Otocoris alpestris*), the compound by the Black Guillemot (*Cepphus grylle*), and there are many species in many families of birds that follow one or the other of these types

of moult. The first annual (a simple or compound juveno-annual) plumage is retained until the first postnuptial moult, but the non-nuptial may be either obliterated by a complete prenuptial moult or more frequently further compounded by the new feathers of a partial renewal. The first non-nuptial therefore is succeeded by a simple first nuptial (juveno-nuptial) as seems to be the case with the Sterninæ, the Bobolink (*Dolichonyx oryzivorus*) and other Passeres, or a compound first nuptial as seen in many widely differing species like the Lapland Longspur (*Calcarius lapponicus*), Bonaparte's Gull (*Larus philadelphia*) or Ruddy Duck (*Erismatura jamaicensis*). This last plumage is perhaps the commonest of the 'immature' plumages, and they are not difficult to understand if we learn their origin. Fortunately for the student most of them are replaced, not later than the first post-nuptial moult by the adult or very nearly adult plumage. Some of the larger Longipennes, Anatidæ and others pass a second year in an 'immature' plumage wholly new at the first post-nuptial moult, but their relative numbers are so small that in some species it is possible they represent birds of deficient vitality, a portion at least seeming to assume adult dress, at a considerably earlier period than is generally supposed.

Much of what I have written will, no doubt, seem obscure and complicated, for the facts about plumages and moults do not readily lend themselves to simple explanation, but in summing up the following systematic arrangement of plumages and moults may perhaps help to make the whole subject clearer.

DERIVATION OF PLUMAGES.

Natal.

Postnatal moult, complete.

Juvenal.

Postjuvenal moult, if complete.

Annual (simple).

Non-nuptial (simple).

Postjuvenal moult, if partial.

Annual (compound).

Natal.

Juvenal.

1st Annual or simple juveno-annual.

1st Non-nuptial or simple juveno-non-nuptial.

1st Annual or compound juveno-annual.

[<i>Lagopus</i> assumes a special protective plumage and by <i>posttutelar moult</i> a compound non-nuptial plumage.]	1st Protective or juveno-tutelar.
Non-nuptial (compound).	1st Non-nuptial or compound juveno-non-nuptial.
<i>Prenuptial moult, if complete.</i>	1st Nuptial or simple juveno-nuptial.
<i>Prenuptial moult, if partial.</i>	1st Nuptial or compound juveno-nuptial.
Nuptial.	
<i>Postnuptial moult complete.</i>	
Annual (simple).	2d or adult Annual or simple annuo-nuptial.
[Some Anatidæ assume a special protective plumage and by <i>posttutelar moult</i> a compound annual plumage.]	2d or adult protective or tutelar.
Non-nuptial (simple)	2d or adult Non-nuptial.
<i>Prenuptial moult if complete.</i>	2d or simple adult Nuptial.
<i>Prenuptial moult, if partial.</i>	2d or compound adult Nuptial.

According to this arrangement of plumages, the old indefinite terms are replaced by exact ones, and instead of 'downy young' we have *natal*, instead of 'first (!)' or 'nestling plumage' we have *juvenal*, and instead of 'autumnal,' 'winter,' 'non-breeding,' 'nuptial' or 'immature' plumages we have the several *annual* or *nuptial* plumages exactly indicated. It is therefore possible to represent the plumage-cycle of a species with considerable accuracy, the following being a few examples.

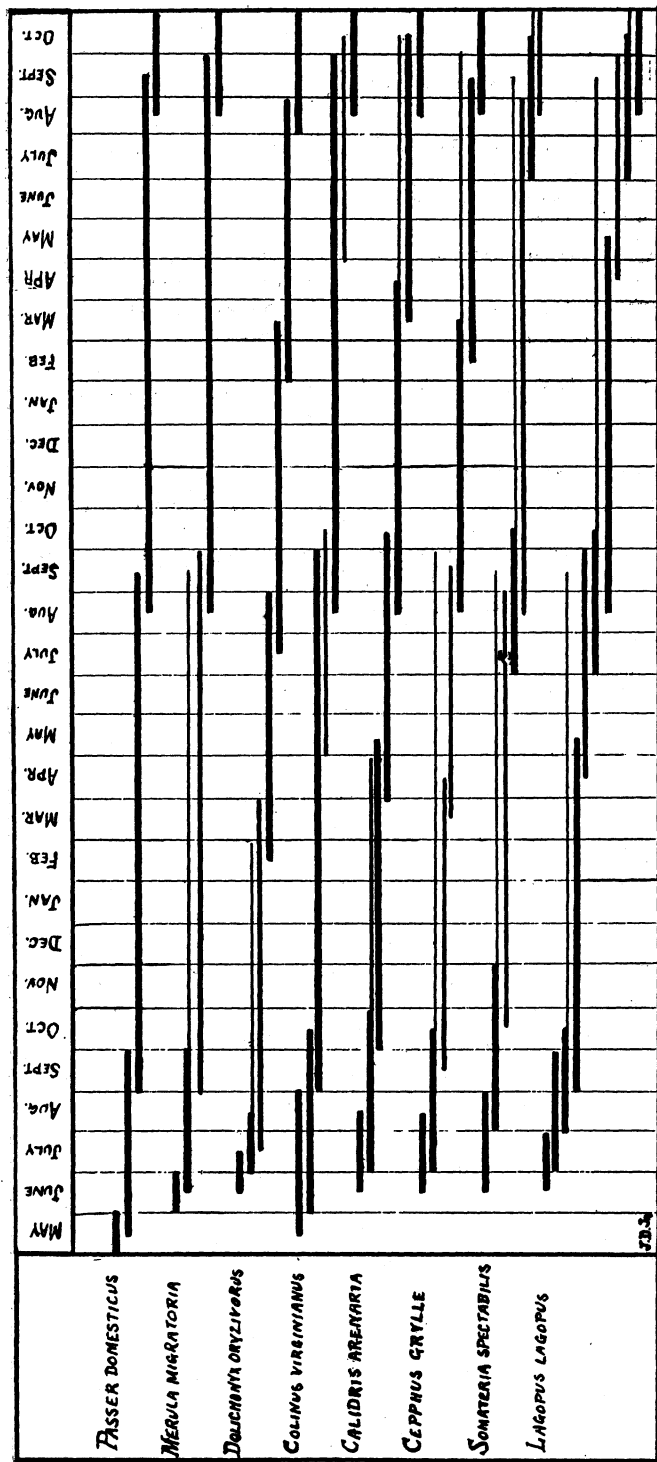
Passer domesticus. Natal, juvenal, simple annual.

Merula migratoria. Natal, juvenal, compound annual.

Carpodacus purpureus. Natal, juvenal, compound first annual, simple adult annual.

Colinus virginianus. Natal, juvenal, simple first non-nuptial, compound nuptial, simple adult non-nuptial.

Dolichonyx oryzivorus. Natal, juvenal, compound first non-nuptial, simple nuptial, simple adult non-nuptial.



A GRAPHIC METHOD OF REPRESENTING PLUMAGES AND MOULTS.

Each line represents a plumage, its beginning, the beginning of the moult by which the plumage is acquired, its end, the end of the moult by which it is lost.

Calidris arenaria. Natal, juvenal, compound first non-nuptial, simple first nuptial, simple second non-nuptial, compound adult nuptial.

Cepphus grylle. Natal, juvenal, compound first non-nuptial, compound nuptial, simple adult non-nuptial.

Somateria spectabilis. Natal, juvenal, compound annual, protective (or tutelar.)

Lagopus lagopus. Natal, juvenal, first protective, compound non-nuptial, compound nuptial, adult protective.

Finally I have prepared a table (p. 254) showing by the graphic method, the plumage-cycles of several species, which differ in the number of plumages worn in equal lengths of time. I have represented the average length of time each plumage is worn and the average time of the beginning of the moults but individuals delayed in moult or deficient in vitality will vary much from the average. To-day the average is none too well known even among the commonest species.

ON THE FINDING OF THE BONES OF THE GREAT AUK (*PLAUTUS IMPENNIS*) IN FLORIDA.

BY O. P. HAY.

ABOUT the beginning of the present year the writer received, for identification, from Prof. W. S. Blatchley, State Geologist of Indiana, a small collection of bones which he had made from an Indian shell heap at Ormond, Florida. In looking over this lot of bones, which in general are those of species living to-day in that region, attention was attracted by a strongly flattened bird humerus. It soon became evident that it belonged to some member of the Alcidae, but was larger than the humerus of any species now living along our coast. On the suggestion of Mr. F. M. Chapman, it was compared with humeri of the Great Auk which had been collected by Prof. F. A. Lucas on Funk Island, and the comparison showed that it agreed with those in every particular. This result